MODELING LIFE STAGE DYNAMICS OF *PSEUDOCALANUS* SPP.

(COPEPODA: CALANOIDA) FROM PRINCE WILLIAM SOUND, ALASKA

By

Natalia M. Pintchouk

RECOMMENDED:

Advisory Committee Chair

Program Head

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

Date

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A

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Natalia M. Pintchouk

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ABSTRACT

A stage at age 1D numerical model (SAGE) was developed to describe reproduction, development, and growth of a group of neritic copepods *Pseudocalanus* spp., and to predict structure and demography of this group. The model tests the relative importance of female abundance, temperature and food on productivity. During spring and the beginning of the summer, stage-specific abundance data from one location in Prince William Sound (PWS), Alaska were available to evaluate the reproductive timing and provide model validation. Development of *Pseudocalanus* spp. was modelled as synchronous, without overlapping broods. Molting costs and assimilation efficiency were estimated from literature data on other calanoid copepods. Wood's population surface method was used to produce a stage at age mortality (SAM) model to evaluate per capita instantaneous stage-specific mortality rates from the field data. The model confirmed the assumption that the abundance of these copepods was controlled by temperature and temporal / stage-to-stage variation in mortality rates, rather than by food availability.

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CHAPTER 1
INTRODUCTION

Zooplankton production models containing age and stage structure are useful in fishery studies because younger stages of many fishes forage on specific life stages. Modeling of life stage dynamics of *Pseudocalanus* spp. (Calanoida, Copepoda) provides information on availability of its early life stages for larval walleye pollock, *Theragra chalcogramma*, and larval Pacific herring, *Clupea palassi.* It is logical to assume that larvae of these two fish species are food limited, yet there is no evidence in the literature to support that contention for Pacific larvae herring. More is known about food selectivity of larval walleye pollock (Hillgruber et al., 1995) and it has been shown that they are food limited at times in Alaskan bays (Clayton et al., 1997).

Pseudocalanus is a genus of small (adult size is about 1 mm) neritic calanoid copepods that is one of the most common zooplankters in the northern oceans. *Pseudocalanus* spp. dominates the zooplankton community of Alaskan bays along with a larger oceanic calanoid copepod, *Neocalanus* spp., and euphausiids (Coyle et al., 1990; Paul and Coyle, 1993).

The life cycle of *Pseudocalanus* spp., like other calanoid copepods, includes six naupliar (NI-NVI) and five copepodite (CI-CV) stages, and adults. The overwintering generation is comprised of fertilized females that do not reproduce until they feed on the spring phytoplankton bloom (Corkett and McLaren, 1978). Adult males do not ascend into the surface layers during the spring bloom (Corkett and McLaren, 1978). Females lay eggs in sacs (clutches), which they carry until hatching occurs. In the laboratory females can reproduce up to ten times (Corkett and McLaren, 1978), but in nature this is rarely achieved due to predation (Ohman and Wood, 1996). At high latitudes, the development of *Pseudocalanus* spp. is synchronous and starts with nearly simultaneous spawning of overwintered females feeding on the spring bloom (Corkett and McLaren, 1978). Each brood

can be traced throughout the reproductive season and subsequent generations do not overlap. Reproduction, embryonic and stage durations of *Pseudocalanus* spp. are temperature dependent (Corkett and McLaren, 1978; Vidal, 1980). Some laboratory experiments show that food limitation may retard development of *Pseudocalanus* spp. (Klein-Breteler, 1982, Green et al., 1991), but most of the authors agree that such low food concentrations rarely occur in nature (Corkett and McLaren, 1978; Frost, 1985; Paul et al., 1990; Huntley and Lopez, 1992). Initial abundance of overwintering fertilized females and stage-specific predation on *Pseudocalanus* spp. appear to be the key factors controlling *Pseudocalanus* spp. abundance (Paul et al., 1990; Ohman and Wood, 1996).

The goal of this work was to model structure and demography of a population of *Pseudocalanus* spp. and investigate the factors controlling reproduction, development, and abundance of this genus. Population abundance data on *Pseudocalanus* spp. were available for several years from one location in Prince William Sound (PWS), Alaska. The data were collected during the spring and early summer, so that salmon hatchery personnel would know when the prey of salmon fry would be plentiful. A coupled 1-D numerical biophysical model of nutrient and plankton dynamics for PWS was developed by Eslinger (1997). The model resolved mixed layer dynamics well; model temperature fields were in a good agreement with field data. The biological components of the model included nitrate, ammonium, and silicon; two phytoplankton species (diatoms, and flagellates) and three zooplankters (*Neocalanus* spp., *Pseudocalanus* spp., and euphausiids). The model accurately simulated the timing and magnitude of the spring phytoplankton bloom. Each of zooplankton group was modeled as one variable and formulated so that each zooplankter was food limited. The physiological effects of temperature on zooplankton were not considered. Unlike the trophodynamic approach used by Eslinger (1997), the hypothesis tested in this study was that reproduction, development and growth of *Pseudocalanus* spp. was temperature-dependent in a food unlimited environment, and that abundance was controlled by temporal and stage-to-stage variations in mortality rates.

The specific objectives were:

- Extend the biophysical model of Eslinger (1997) to a stage at age (SAGE), temperature-dependent 1D numerical model of *Pseudocalanus* spp. reproduction, development and growth.
- Using Belehradec's function of temperature and temperature data from the euphotic zone (Ohman and Wood, 1996), a) estimate the age structure of the population, and the time between successive broods, b) identify subsequent broods in the field data; c) estimate timing of egg production around model day 0; and d) estimate initial abundance of reproductive females from the field data. If field data indicate that *in situ* reproduction began before model day 0 (Julian day 70), introduce an initial population size structure.
- Use SAGE to estimate the frequency of clutches over time and generate missing data on egg production from adult female abundance, assuming that the number of eggs per clutch is equal to the reported mean of 16 (Corkett and McLaren, 1978).
- Use the population surface method of Wood (Wood,1994; Ohman and Wood, 1996) to develop a stage-at-age model (SAM) for estimating daily stage-specific mortality rates from the field data.
- Based on literature data on reproduction of *Pseudocalanus* spp., perform model sensitivity analysis for such reproductive parameters as number of eggs per clutch and number of clutches produced. Generate egg abundance data with the best estimates for the number of eggs per clutch and run SAM with this data to obtain improved estimates of stage-specific daily mortality rates.
- Test the sensitivity of the model to the initial abundance of reproductive females.
- Test the sensitivity of the model to several sets of values of stage-specific daily mortality rates.
- From a balance equation for growth, excretion, egestion rates and molt costs, estimate the amount of phytoplankton grazed by the model population of *Pseudocalanus* spp.

CHAPTER 2
MATERIALS AND METHODS

Study site and structure of the data

Time-series, size-structured data on abundance (numbers per m^3), and biomass (mg live weight per m^3) of *Pseudocalanus* spp. were available for March - mid July from the AFK hatchery located on Evans Island, Prince William Sound (PWS), Alaska (Figure 2.1). Evans Island is situated near Montague Strait, which is a part of the Alaska Coastal Current. The Alaska Coastal Current has a maximum signal in fall and winter, resulting in renewal of PWS water at least twice, and 40% of PWS is renewed during spring and early summer (Niebauer et al., 1994).

Vertically integrated zooplankton samples were collected from the upper 50 m of water column using a 333 µm mesh net. This mesh size did not capture the naupliar stages and undersampled early copepodite stages (CI-CIII). Live weights (mg) of *Pseudocalanus* spp. were available for copepodites and adults from the AFK hatchery data. Live naupliar weights for *Pseudocalanus* spp. were not available for PWS. They were set after Hay and Evans (1988) but 2.5 greater, as estimated weights for PWS copepodite stages and adult animals were about 2.5 times higher than corresponding weights for Atlantic *Pseudocalanus* spp. (Table 2.1).

Model time step and spatial resolution

This *Pseudocalanus* spp. stage-specific numerical model is an extension of the 1D coupled physical-biological numerical model developed by Eslinger (1997) for PWS. The model has 2 m vertical resolution (a 50 layer model) and a 2 hrs time step. *Pseudocalanus* spp. inhabited the upper 40 m of model water column.

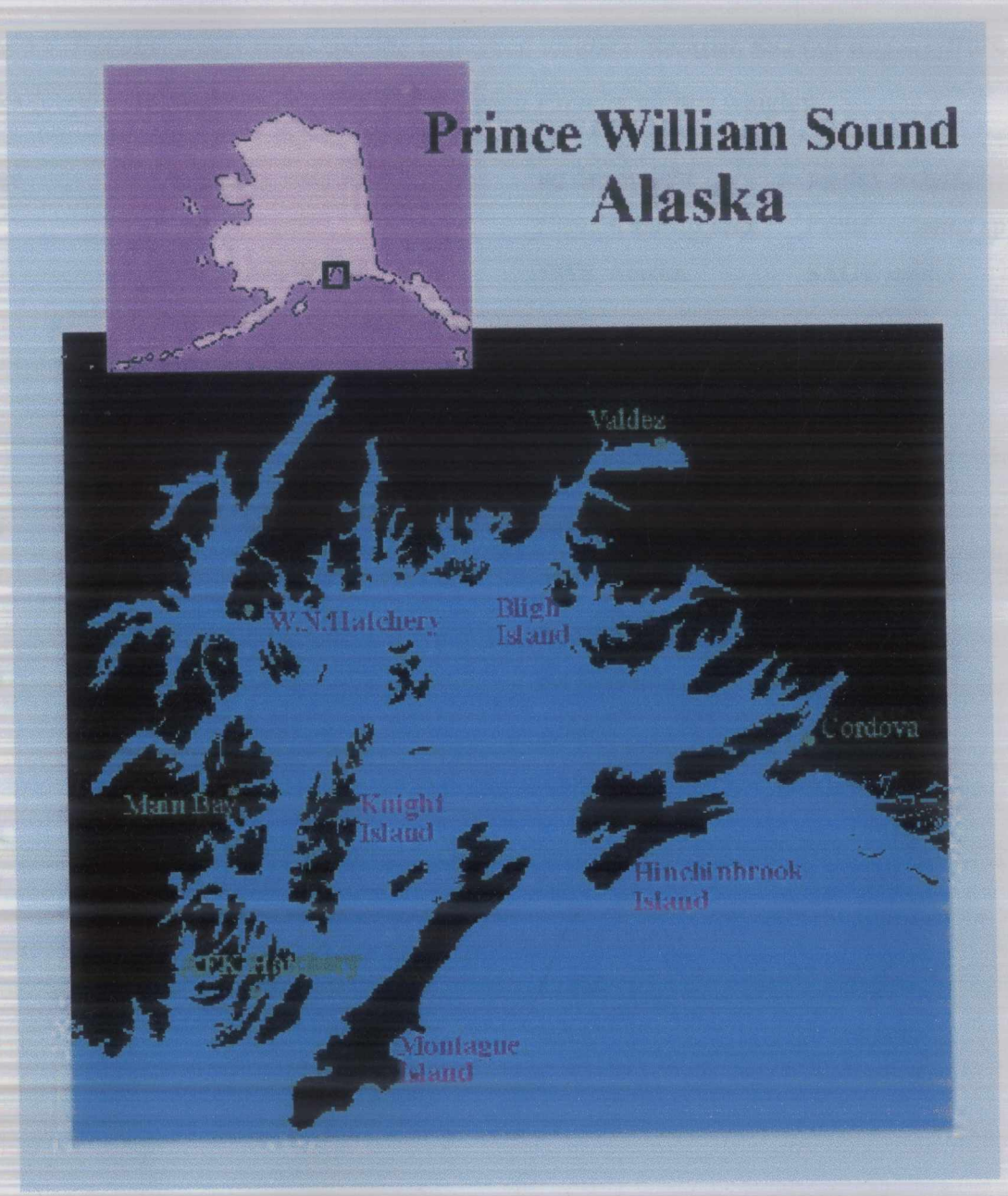

Figure 2.1. Map of Prince William Sound, Alaska.

Table 2.1. *Pseudocalanus* stage-specific individual weights: Scottish Sea (all stages); PWS, Alaska (copepodits and adults); and SAGE mean *Pseudocalanus* weights.

Stage	µg dry weight, *P. elongatus*, Scottish Sea*	µg dry weight, *Pseudocalanus* spp. PWS, Alaska**	µg dry weight, *Pseudocalanus* spp. SAGE model***
Egg	0.304	not avaiable	0.760
NI	0.304	not available	0.760
NII	0.367	not available	0.918
NIII	0.498	not available	1.246
NIV	0.616	not available	1.540
Nv	0.730	not available	1.826
NVI	0.809	not available	2.022
Ci	0.551	1.650	1.650
CII	1.134	2.850	2.850
CIII	2.128	5.294	5.294
CIV	3.712	7.950	7.950
CV	5.968	13.126	13.126
AF	10.349	31.350	31.350
AM	5.339	9.900	9.900

* from Hay and Evans (1988).

** Coyle, Cooney , personal communication.

*** SAGE stage-specific individual weights for egg and nauplii were set after Hay and Evans (1988) but 2.5 higher.

Temperature fields

Temperature (Figure 2.2.A), at 2-hr intervals and 2-m vertical resolution, was calculated from Eslinger's (1997) mixed layer model and was used to simulate temperature-dependent reproduction, development, and growth of *Pseudocalanus* spp. in the SAGE model. Figure 2.2.B shows field (CLAB) temperatures, and there was a good agreement between field (Figure 2.2.B) and model (Figure 2.2.A) temperatures over the study period.

Life cycle of Pseudocalanus spp.*: model structure*

Pseudocalanus spp. development includes six naupliar (NI-NVI), five copepodite (CI-CV) stages, and adults. Females carry egg sacs until they hatch. Well fed females, in the absence of predators, produce eight to ten clutches before senescence (Corkett and McLaren, 1978). In high latitudes, the development of *Pseudocalanus* spp. is synchronous; overwintering females reproduce after feeding on the spring phytoplankton bloom (Corkett and McLaren, 1978). In the laboratory the time between subsequent clutches was found to be 1.25 times that of the embryonic duration (ED), but it may be somewhat longer in nature (Corkett and McLaren, 1978). Development was not isochronal; duration of the longest stage (NIII) for Atlantic *Pseudocalanus* spp. was estimated to be equal to 1.46ED (Corkett and McLaren, 1978). Cohorts can be traced in samples, i.e., subsequent broods do not overlap. In the model, stage durations (SD) were set after Corkett and McLaren (1978) and were proportional to the ED with proportionality constants as for the Atlantic group of species and equal to 0.18, 0.37, 1.46, 0.81, 0.69, 0.4 (NI-NVI stages); and 1.23, 1, 0.98, 1.02, 1.32 (CI-CV stages). To avoid temporal overlap between broods, time between successive clutches was set equal to 1.5ED, which was longer than the duration of the longest development stage. This value was found from the best fit of the model output to the data. *Pseudocalanus* spp. was modeled using three variables: abundance, individual weight, and population biomass.

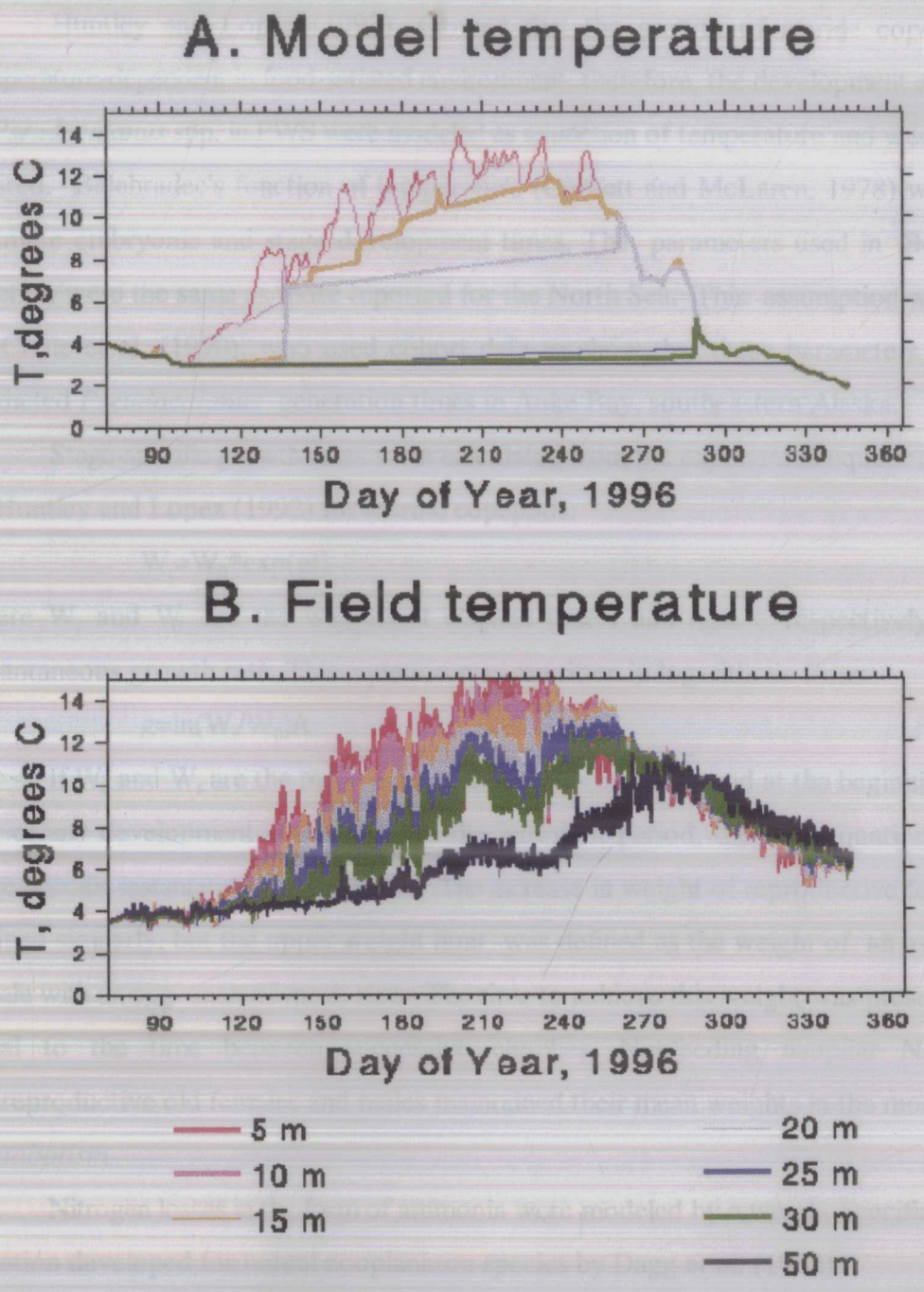

Figure 2.2. Model temperature (A) and *in situ* (C-LAB) measured temperature (B) in 1996 (Eslinger, 1997).

Development and growth of Pseudocalanus spp.: model formulation

Huntley and Lopez (1992), showed that the growth of marine copepods was temperature-dependent in food-satiated environment, therefore, the development and growth of *Pseudocalanus* spp. in PWS were modeled as a function of temperature and were not food limited. Belehradec's function of temperature (Corkett and McLaren, 1978) was used to estimate embryonic and stage development times. The parameters used in Belehradec's function were the same as those reported for the North Sea. This assumption was verified by Coyle et al. (1990), who used cohort data to show that these parameters accurately predicted *Pseudocalanus* generation times in Auke Bay, southeastern Alaska.

Stage-specific growth rates were calculated from the exponential equation proposed by Huntley and Lopez (1992) for marine copepods:

$$W_t=W_0*\exp(gt)$$

where W_t and W_0 are the weights at elapsed time t and time t respectively, and g is instantaneous growth rate. This equation was rewritten in logarithmic form:

$$g=\ln(W_t/W_0)/t$$

If W_0 and W_t are the mean individual weights of a copepod at the beginning and the end of any development stage, and t is the intermolt period, then the equation describes stage-specific instantaneous growth rate. The increase in weight of reproductive females was defined similarly, but the upper weight limit was defined as the weight of an average size female with an egg sack of mean size. The time to achieve this weight was presumed to be equal to the time between successive clutches. Nonfeeding naupliar NI-NII and nonreproductive old females and males maintained their mean weights in the model.

Metabolism

Nitrogen losses in the form of ammonia were modeled by a weight-specific empirical equation developed for boreal zooplankton species by Dagg et al. (1982):

$$U=0.072*W(t)^{.902}$$

where U is in gN per body weight of animal per day, and W(t) is weight of the animal in gN

at time t. Assimilation efficiency was set equal to 70% as reported for the herbivorous zooplankton (Conover, 1968). Assimilation rates were calculated on a stage-specific basis as the sum of growth and excretion rates. Vidal (1980b) estimated for *C. pacificus* that molting costs were between 2 and 0.2% of carbon content of body weight. In the model this was set to 0.2% of *Pseudocalanus* spp. carbon content of body weight.

Size-structure of the population and stage-specific mortality

The limited population structure data from AFK field data and the modeled temperature fields were used to calculate 1) the complete time-dependent population structure and 2) time-varying stage-specific instantaneous mortality rates as part of Stage-at-Age Mortality (SAM) model. Wood (1994) and Ohman and Wood (1996) provided a detailed description of the method, which is summarized below.

The calculations require estimates of the age of animals at field sample times and egg abundance data, neither of which were directly measured. Only copepodite stages IV-V and adult animals were sampled accurately at the AFK. Given these populations at each sampling time, and the temperature history before that time, the age structure of the population could be etsimated using Belehradec's function (Ohman and Wood, 1996). No *in situ* data on egg abundance were available. Therefore, the frequency of clutch production over a sample period was also estimated from the Belehradec's temperature function. From the clutch frequency and the measured abundance of adult females, egg abundance was calculated.

A bicubic interpolation was performed on the estimated egg abundance and copepodite abundance and age data (knots in abundance-age-time space) to find the population surface (Figure 2.3.A). From changes in the population surface, the stage specific, instantaneous mortality rates were calculated (Figure 2.3.B) by solving the McKendric-von Foerster equation for mortality:

$$(\partial S/\partial t) + (\partial S/\partial a) + MS = 0$$

where S(a,t) (population surface) is the number of individuals of age a, at time t, and M(a,t)

is the mortality rate of individuals of age a, at time t.

Model initialization

Meteorological data for the physical oceanographic model and AFK hatchery zooplankton data for the biological model were not available before early March, so the model day 0 was set at Julian day 70 (March 11). Day 0 values were based on the observed population structure of *Pseudocalanus* spp. at the PWS hatchery site on the first sampling day. The *in situ* abundance data included adult females and males, and copepodite stages CI-CV. The cohort analysis of the field data indicated that reproduction had begun before model day 70. From the temperature data, the generation time of those first broods was estimated; the broods produced prior to day 70 had already progressed to the early naupliar stages. Their abundance was estimated from the output of the SAM model, and these numbers were used as input to the model as well (Table 2.2).

A summary of all model equations is given in Table 2.3.

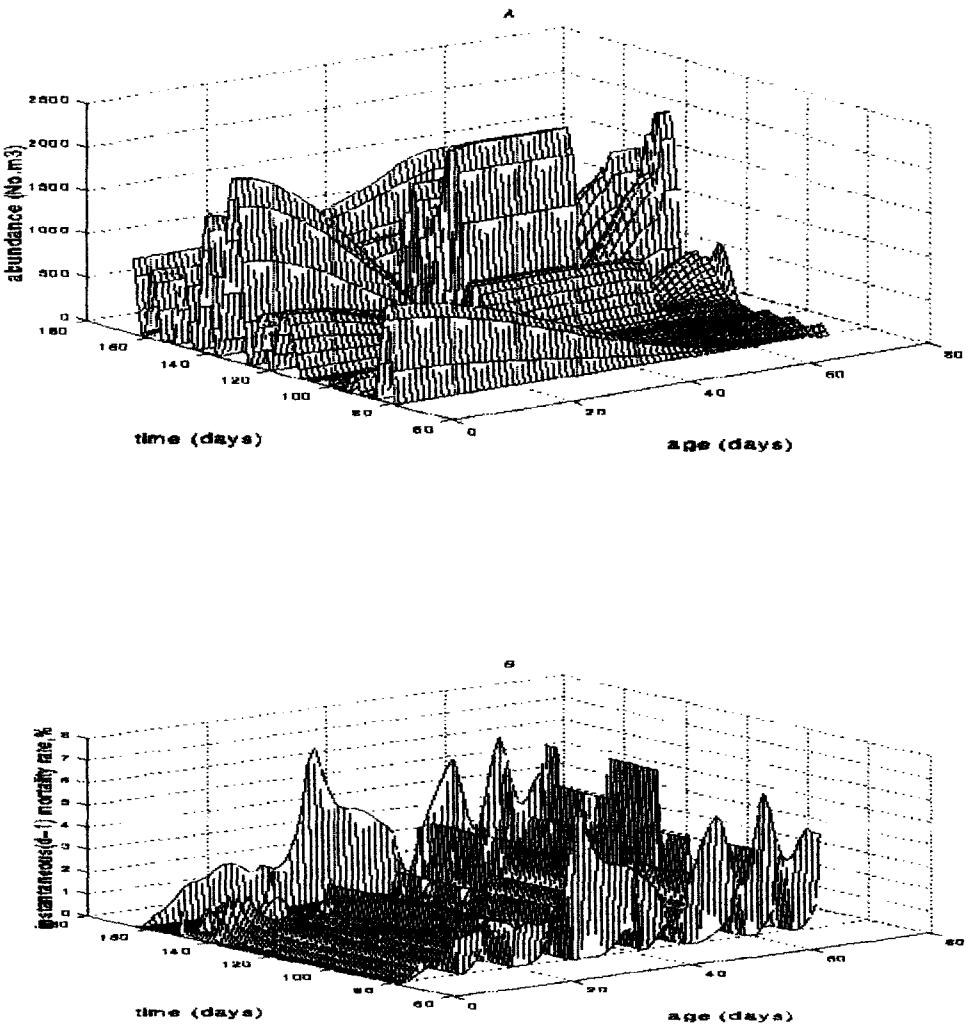

Figure 2.3.A. Approximation to a population surface for preadult individuals of the AFK hatchery population of *Pseudocalanus* spp. per unit age interval in 1996, and B) corresponding instantaneous mortality rates (d^{-1}) estimated from SAM model.

Table 2.2 Initial values for *Pseudocalanus* spp. abundance, at AFK hatchery, PWS, Alaska, 1996.

Input day (Julian)	Life Stage	No.(m^{-3})
78	NIV	600 *
70	NVI	37 *
84	CI	76 *
82.6	CIII	34 *
85	CV	41
70.5	AF	73
79.0	AM	21

* Abundance estimated from the SAM model

Table 2.3. Summary of SAGE and SAM model equations describing life cycle, reproduction, development, growth and mortality of *Pseudocalanus* spp. in PWS, Alaska.

horizontal dimension -point
vertical dimension, 20 layers, 2m resolution: z {1,20}

age class index: k {egg, NI, NII, NIII, NIV, NV, NVI, CI, CII, CIII, CIV, CV, adult reproductive females, adult males, adult not reproductive females}

state variables:

$B_{z,k}$

$$dB_{z,k} = g_{z,k}W_{z,k}N_{z,k}dt +$$

net growth

$$+ (1\text{-}m)N_{z,k-1}W_{z,k-1}|t=SD_{z,k} - (1\text{-}m)\,N_{z,k}W_{z,k}|t=SD_{z,k+1} -$$

molting from the previous stage molting into the next stage

$$- M_kN_{z,k}W_{z,k}dt$$

mortality

$I_{z,k}$

$dI_{z,k} = \{g_{z,k}W_{z,k}N_{z,k} +$

net growth

$+e1W_{z,k}^{e2}N_{z,k} +$

excretion

$+ aS(g_{z,k}W_{z,k}N_{z,k}+e1W_{z,k}^{e2}N_{z,k})\}dt +$

egestion

where

$g_{z,k} = \log_e(W_{z,k}/W_{z,k-1})/SD_{z,k}$

$SD_{z,k} = vED_z$

$ED_z = 1845(T_z + 11.45)^{-2.05}$

v { 1, .18, .37, 1.46, .81, .69, .4, 1.23, 1, .98, 1.02, 1.32}

m = 7E-3

e1 = 9.15E-4

e2 = .902

aS = 3/7

$M_k = -(\partial S/\partial t + \partial S/\partial a)/S(a, t),\ k <= CV$

$M_k = (1/N_{z,k}(t))(R(t)- dN_{z,k}(t)/dt),\ k = \{AF, AM\}$

$R(t) = S(a_M,t)(1-da_M/dt)$

Legend

$B_{z,k}$	stage-specific population biomass	[mMN/m^3] , [mg live weight/m^3] , [mgC/m^3]
$I_{z,k}$	total phytoplankton grazed	[mMN/m^3] , [mg live weight/m^3] , [mgC/m^3]
$W_{z,k}$	stage-specific individual weight	[mMN] , [mg live weight]
$N_{z,k}$	abundance	[number of individuals/m^3]
dt	model time step	[2 hrs]
$g_{z,k}$	growth rate	[hr^{-1}]
$SD_{z,k}$	stage duration	[hr]
v	multiplier constant of stage duration	
$ED_{z,}$	embryonic duration	[hr]
T_z	temperature	[C^o]
m	molting rate, % body nitrogen content (converted from % carbon content)	
e1, e2	constants of the exponential equation of excretion	
aS	egestion constant, % of grazed phytoplankton, unassimilated	
M_k	instantaneous mortality rate	[hr^{-1}]
a	age of animals	
a_m	age of animals at maturation boundary	
S(a, t)	population surface, i.e. number of individuals of age a, at time t	

CHAPTER 3

RESULTS

Population dynamics

The field data and the results of SAGE and SAM models are shown in Figure 3.1. The best model estimates for the number of egg clutches laid by each female generation and the number of eggs per clutch were 8, and 5, respectively. These predictions fall well within the reported ranges for *Pseudocalanus* spp. (Corkett and McLaren, 1978; Paul et. al., 1990). SAGE estimates of total abundance of stages CIV, CV, and adult females showed good agreement with the field data. I compared the modeled and field abundances for these specific stages because the 333 μm mesh was adequate for sampling them. Estimated abundance for all feeding stages is also shown on the plot. SAGE and SAM estimates of abundance for adult females and for copepodite stages CV and CIV were in a good agreement with field data. However, modeled abundance of copepodite stage CIV was higher for days 135-150 than observed. SAM estimates for missing naupliar and undersampled younger copepodite stages were interpolated from the estimated egg abundance and *in situ* abundance of CIV, CV, and adult females, and might not have been estimated accurately.

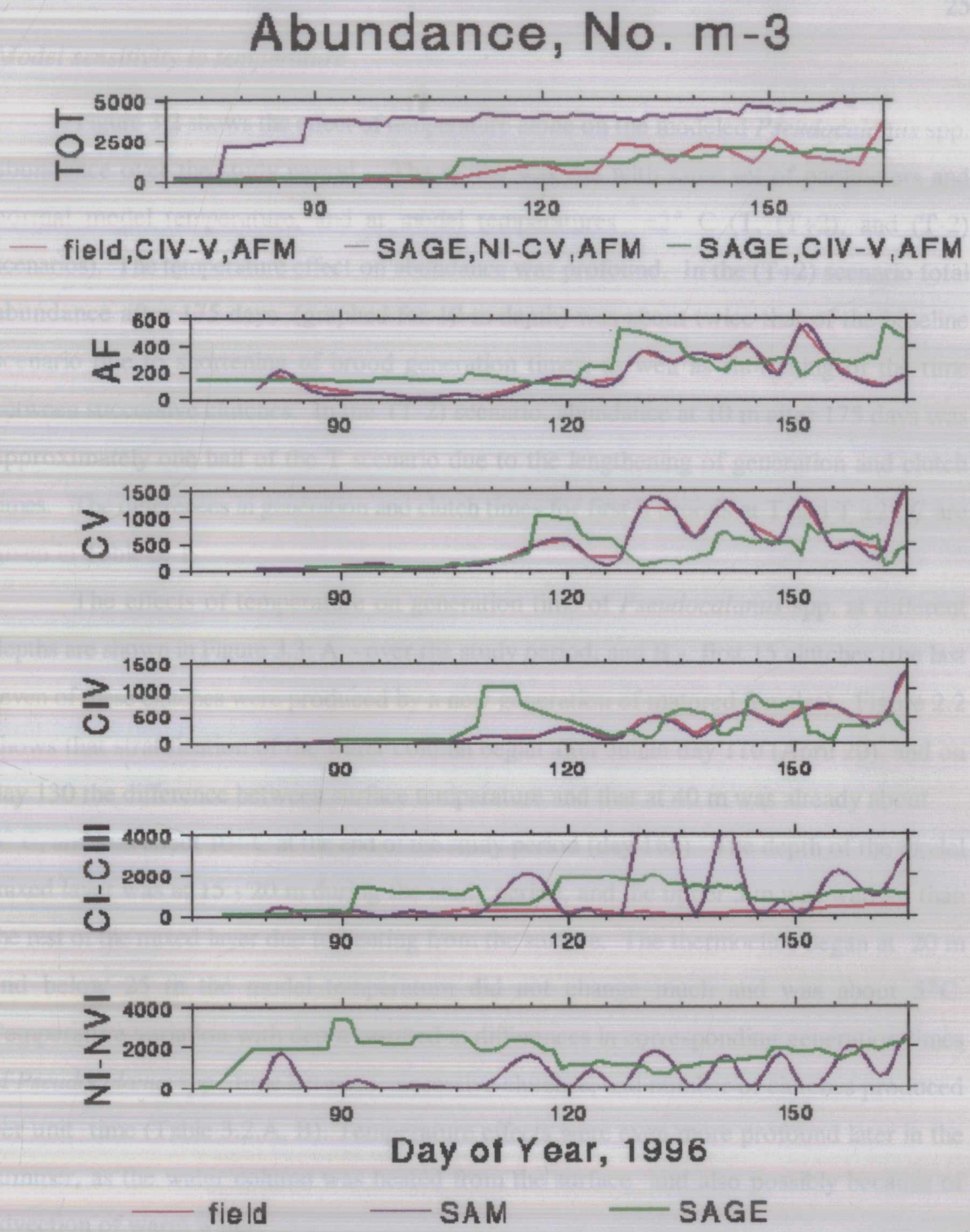

Figure 3.1. Abundance of life stages of *Pseudocalanus* spp.: results from SAGE, SAM, and field data.

Model sensitivity to temperature

Figure 3.2 shows the effect of temperature alone on the modeled *Pseudocalanus* spp. abundance over the study period. The model was run with same set of parameters and normal model temperature, and at model temperatures ±2° C (T, (T+2), and (T-2) scenarios). The temperature effect on abundance was profound. In the (T+2) scenario total abundance after 175 days (graphed for 10 m depth) was about twice that of the baseline scenario due to shortening of brood generation times, as well as shortening of the time between successive clutches. In the (T-2) scenario, abundance at 10 m after 175 days was approximately one half of the T scenario due to the lengthening of generation and clutch times. The differences in generation and clutch times for first 5 broods at T and T ±2° C are given in Table 3. 1.

The effects of temperature on generation time of *Pseudocalanus* spp. at different depths are shown in Figure 3.3: A - over the study period, and B - first 15 clutches (the last seven of these clutches were produced by a new generation of matured females). Figure 2.2 shows that stratification of the water column began after Julian day 110 (April 20), and on day 130 the difference between surface temperature and that at 40 m was already about 5° C, and was about 10° C at the end of the study period (day 165). The depth of the model mixed layer was at 15 - 20 m during the study period, and the upper 5 m was warmer than the rest of the mixed layer due to heating from the surface. The thermocline began at 20 m and below 25 m the model temperature did not change much and was about 5°C. Temperature variation with depth resulted in differences in corresponding generation times of *Pseudocalanus* spp., time between successive clutches, and number of clutches produced per unit time (Table 3.2.A, B). Temperature effects were even more profound later in the summer, as the water column was heated from the surface and also possibly because of advection of warm water.

Model sensitivity to reproduction parameters

The number of eggs in a clutch was the parameter to which the SAGE and SAM abundance estimates for *Pseudocalanus* spp. were most sensitive. Figure 3.4.A (SAM, naupliar stages and SAGE, all stages) shows SAGE and SAM output when the number of eggs in a clutch was set to the maximum, mean and minimum values reported for Atlantic *Pseudocalanus* spp., i.e., 32, 16, or 3 respectively (McLaren, 1978). At 32 eggs per clutch, abundance was about two times higher, and at 3 eggs per clutch about ten times lower, than that at 16 eggs per clutch. Five eggs per clutch was the estimate of this parameter which provided good agreement between SAGE, SAM, and field observations (Figure 3.1). Generated egg abundance data, with number of eggs per clutch equal to 5, was used as input into the SAM model, and SAM output of that particular set of stage-specific instantaneous mortality rates was used as input into the SAGE model, which was run with number of eggs per clutch equal 5.

The number of clutches produced by females and the initial female abundance were also influential parameters. Figure 3.4.B shows SAGE output for total *Pseudocalanus* abundance with the number of eggs per clutch equal to 5, and the number of clutches produced by a female equal to 10, 8, or 6. The first 6 clutches were produced by the overwintered generation (G0) up to day 150; after this day the productivity was two to three times higher, when females produced two and four more clutches, respectively, due to higher frequency of clutches and decreasing generation times as temperature increased.

Figure 3.4.C shows the SAGE output for total *Pseudocalanus* abundance when the initial abundance of females was set equal to that of the first sampling day in the data set, and increased, or decreased by a factor of two. Higher initial abundance of overwintered females resulted in higher population biomass later in spring and summer, and vice versa.

Table 3.1. SAGE sensitivity to temperature over the study period: generation and clutch times for the first 5 broods produced *in situ* (10 m depth) at T, and T ±2° C.

	1st brood matured on day	Broods 2 3 4 5 were produced on day	Broods 2 3 4 5 and their estimated generation time (days)
T°	138	82 92 104 114	60 57 55 52
T+2°	127	79 88 96 105	60 56 50 44
T-2°	140	85 100 116 132	77 - - - *

* Broods 3, 4, and 5 did not compete development by the end of the study period at (T-2)-scenario.

Table 3.2.A. SAGE estimated generation times for *Pseudocalanus* spp. from different depths during first 165 days and number of broods matured by day 165.

5 m depth	10 and 15 m depth	20 m depth	25-40 m depth
5 broods matured	4 broods matured	3 broods matured	2 broods matured

Tab. 3.2.B. SAGE estimated maturation times for first 15 clutches of *Pseudocalanus* spp. from different depths.

5 m depth	10 and 15 m depth	20 m depth	25-40 m depth
By day 200	By day 205	By day 230	By day 285

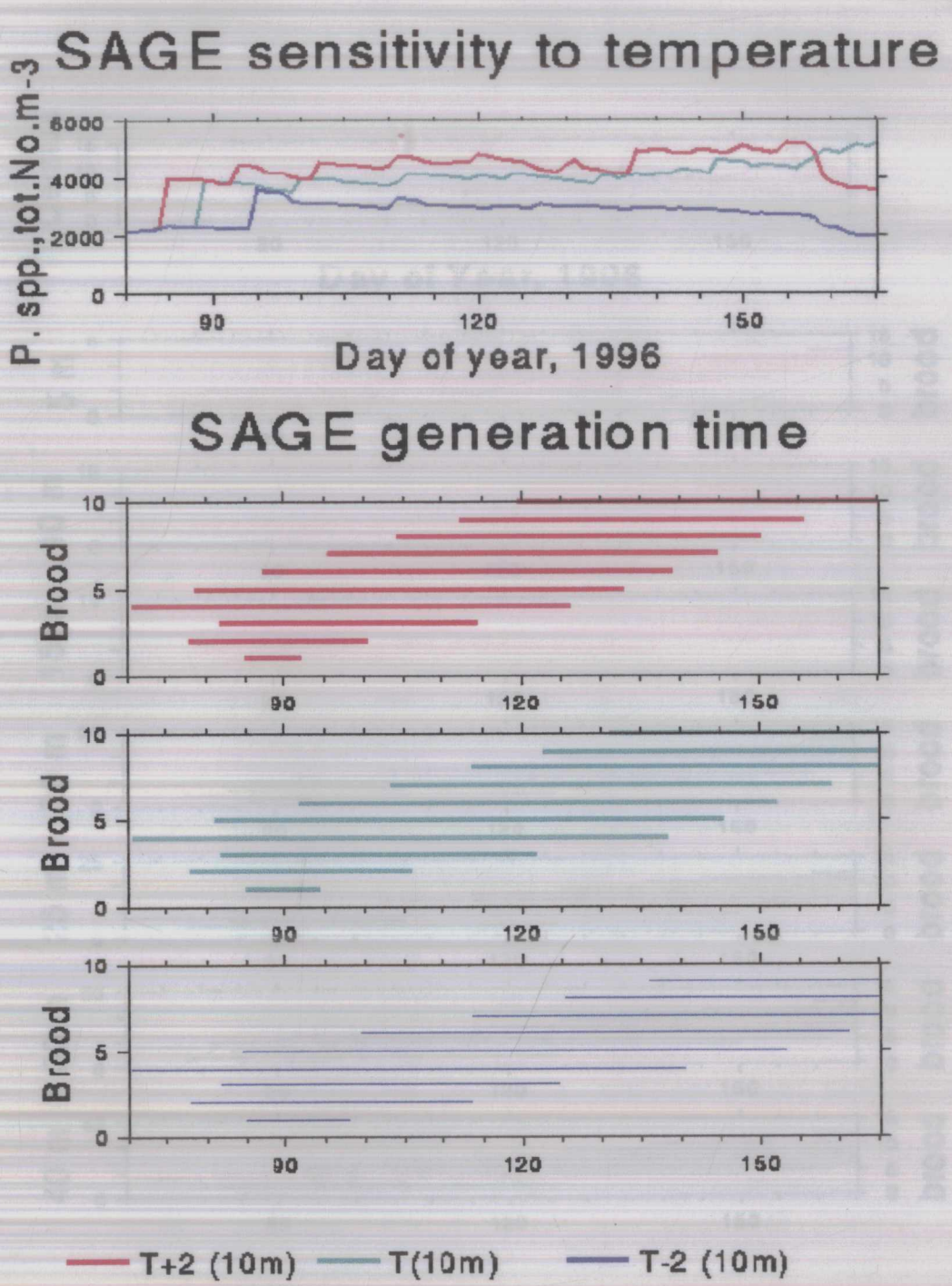

Figure 3.2. SAGE sensitivity to temperature over the study period; total abundance and estimated generation time of *Pseudocalanus* spp. at 10 m depth for normal model temperature, and for 2^0 C higher and lower than normal.

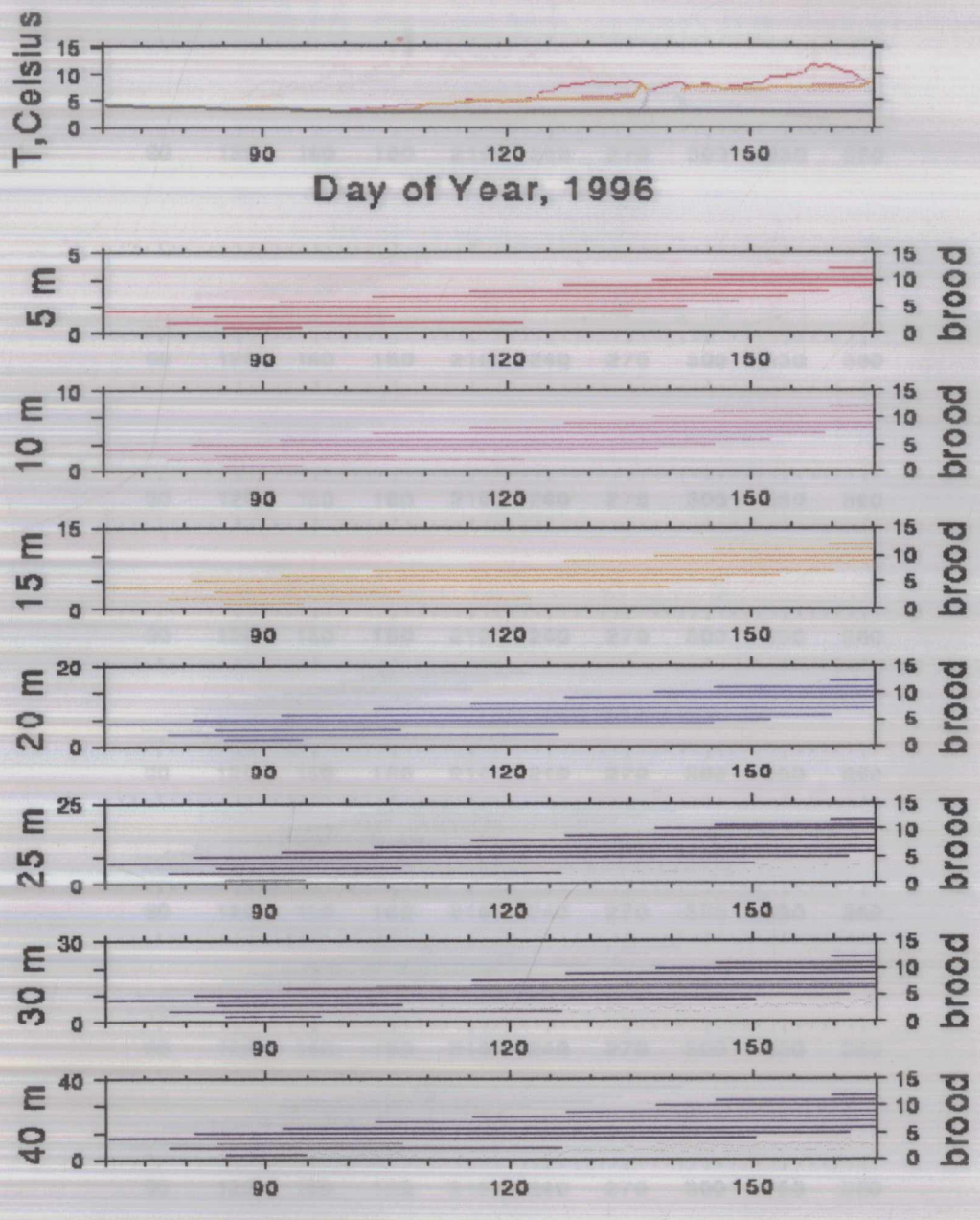

Figure 3.3.A. SAGE estimated generation times for *Pseudocalanus* spp. from different depths during the first 165 days.

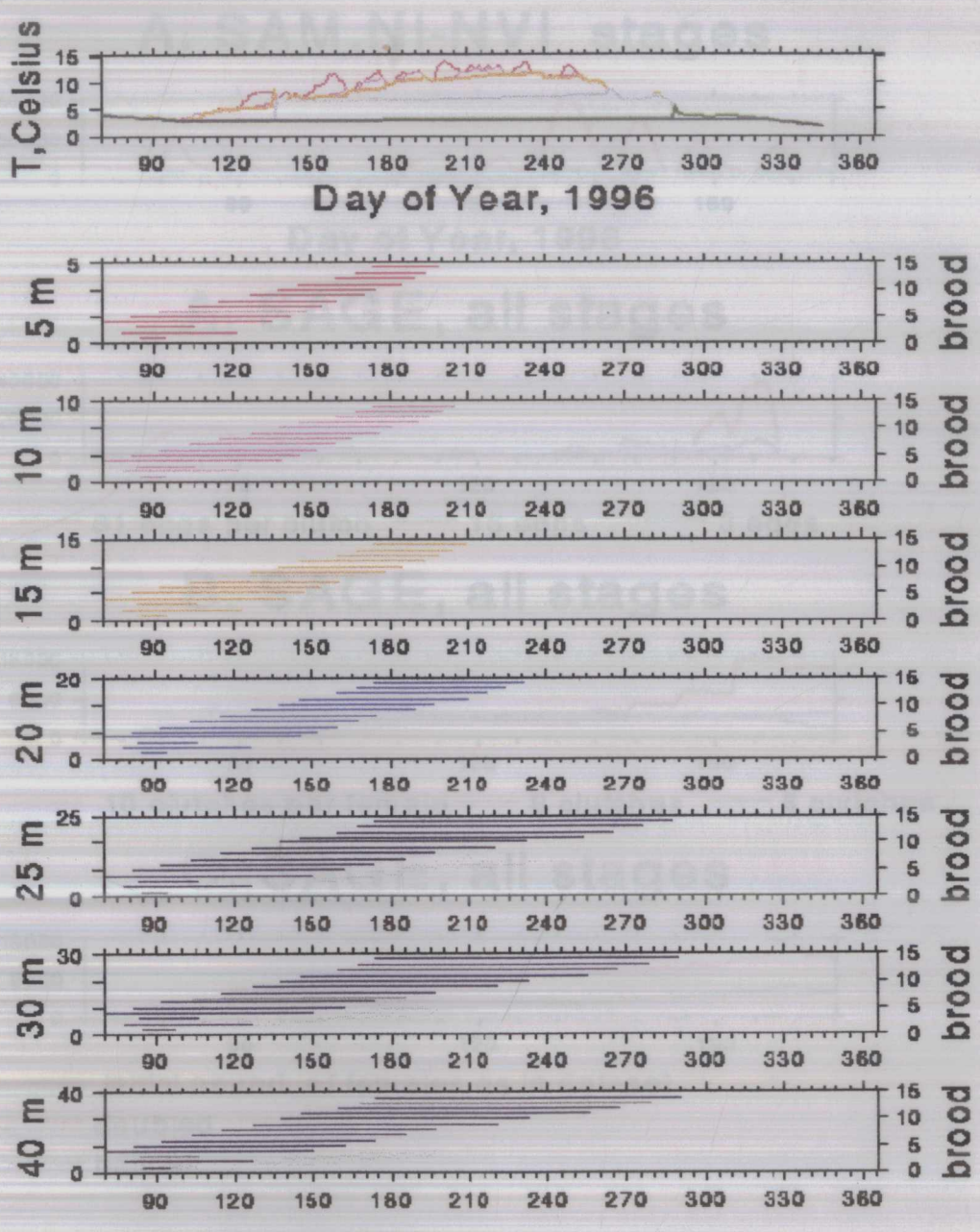

Figure 3.3.B. Same as for Figure 3.3.A, but for an annual basis showing the first fifteen clutches produced *in situ.*

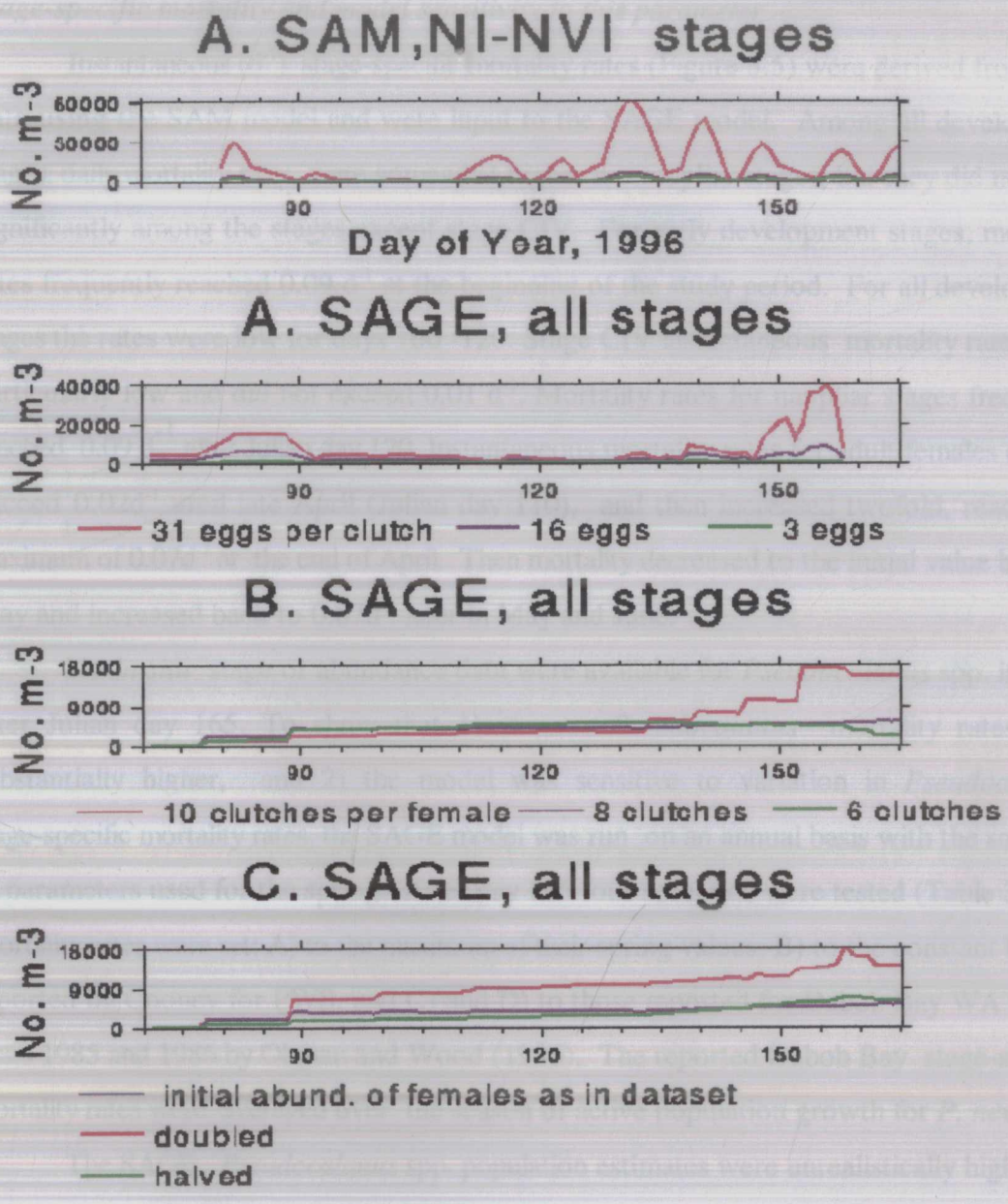

Figure 3.4. Model sensitivity to reproduction parameters: A) number of eggs per clutch; B) number of clutches per female; C) model sensitivity to initial abundance of reproductive females.

Stage-specific mortality and model sensitivity to this parameter

Instantaneous (d^{-1}) stage-specific mortality rates (Figure 3.5) were derived from field data using the SAM model and were input to the SAGE model. Among all development stages, daily mortality rates were somewhat higher for naupliar stages, but they did not vary significantly among the stages except stage CIV. For early development stages, mortality rates frequently reached 0.09 d^{-1} at the beginning of the study period. For all development stages the rates were low for days 100 -120. Stage CIV instantaneous mortality rates were particularly low and did not exceed 0.01 d^{-1}. Mortality rates for naupliar stages frequently reached 0.09 d^{-1} after Julian day 120. Instantaneous mortality rates for adult females did not exceed 0.02d^{-1} until late April (Julian day 110), and then increased twofold, reaching a maximum of 0.07d^{-1} at the end of April. Then mortality decreased to the initial value by mid-May and increased back to 0.07d^{-1} later in May and June.

No *in situ* stage or abundance data were available for *Pseudocalanus* spp. in PWS after Julian day 165. To show that 1) summer *Pseudocalanus* mortality rates were substantially higher, and 2) the model was sensitive to variation in *Pseudocalanus* stage-specific mortality rates, the SAGE model was run on an annual basis with the same set of parameters used for the spring. After day 165 four scenarios were tested (Table 3.3). Mortality rates were set: A) to the maximum of their spring values; B) to the constant 0.06d^{-1} reported by Cooney for PWS, and C) and D) to those reported for Dabob Bay WA for the years 1985 and 1986 by Ohman and Wood (1996). The reported Dabob Bay stage-specific mortality rates were averaged over the season of active population growth for *P. newmani.*

The SAGE *Pseudocalanus* spp. population estimates were unrealistically high when SAGE ran with field derived stage-specific spring mortality values (Figure 3.6.A). When the model was ran with the constant 0.06d^{-1}, several periods of increased *Pseudocalanus* abundance were observed after day 180, as new broods matured and became reproductive. Reported mortality rates for the Dabob Bay population of *P. newmani* were higher for all stages for 1986, and SAGE abundance of *Pseudocalanus* spp. was lower when the model

was run with this set of values, than with year 1985 values (Figure 3.6.C). Dabob Bay rates for both years were high for the PWS *Pseudocalanus* population and resulted in extinction of the population by day 270.

Food availability

Although there was not always a good agreement between the stage-specific SAGE model and field abundance data (Figure 3.1), the total SAGE estimated biomass of *Pseudocalanus* spp. agreed well with the field data during the spring bloom (Figure 3.7.A). Figure 3.7.B shows SAGE estimated metabolic rates (per model step, 2 hrs) of the total *Pseudocalanus* spp. The ingestion rate was estimated from the balance equation as the sum of net growth rate, excretion rate, and egestion rate, and molting costs. Figures 3.7.B and C show estimated metabolic costs, in mg C m^{-2} d^{-1} and in percent of body weight^{-1} d^{-1}, respectively.

Figure 3.8.A shows field and model phytoplankton biomass (mg Chl m^{-3}). SAGE, total consumption of phytoplankton by *Pseudocalanus* is shown in Figure 3.8.B (mg Chl $m^{-3}d^{-1}$), which was a small fraction of model phytolankton biomass (Figure 3.8.C) over the study period. Then the ratio increased as model phytoplankton concentration became very low (for days 240-300). Field data, however, indicated that phytoplankton was abundant over this period of time, but phytoplankton species composition was unknown, as only fluorescence data were available.

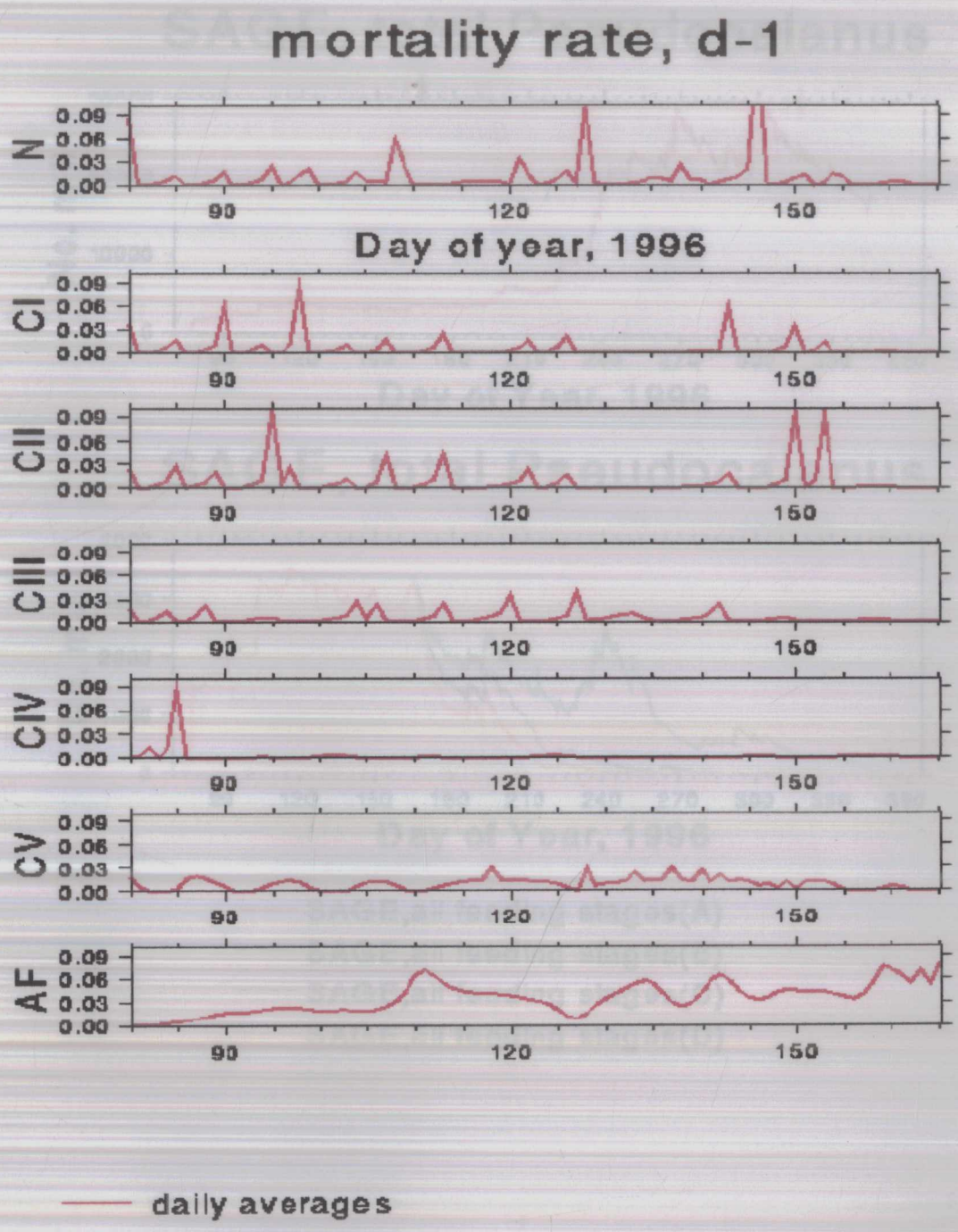

Figure 3.5. SAM estimated instantaneous (d^{-1}) stage-specific mortality rates for *Pseudocalanus spp.*

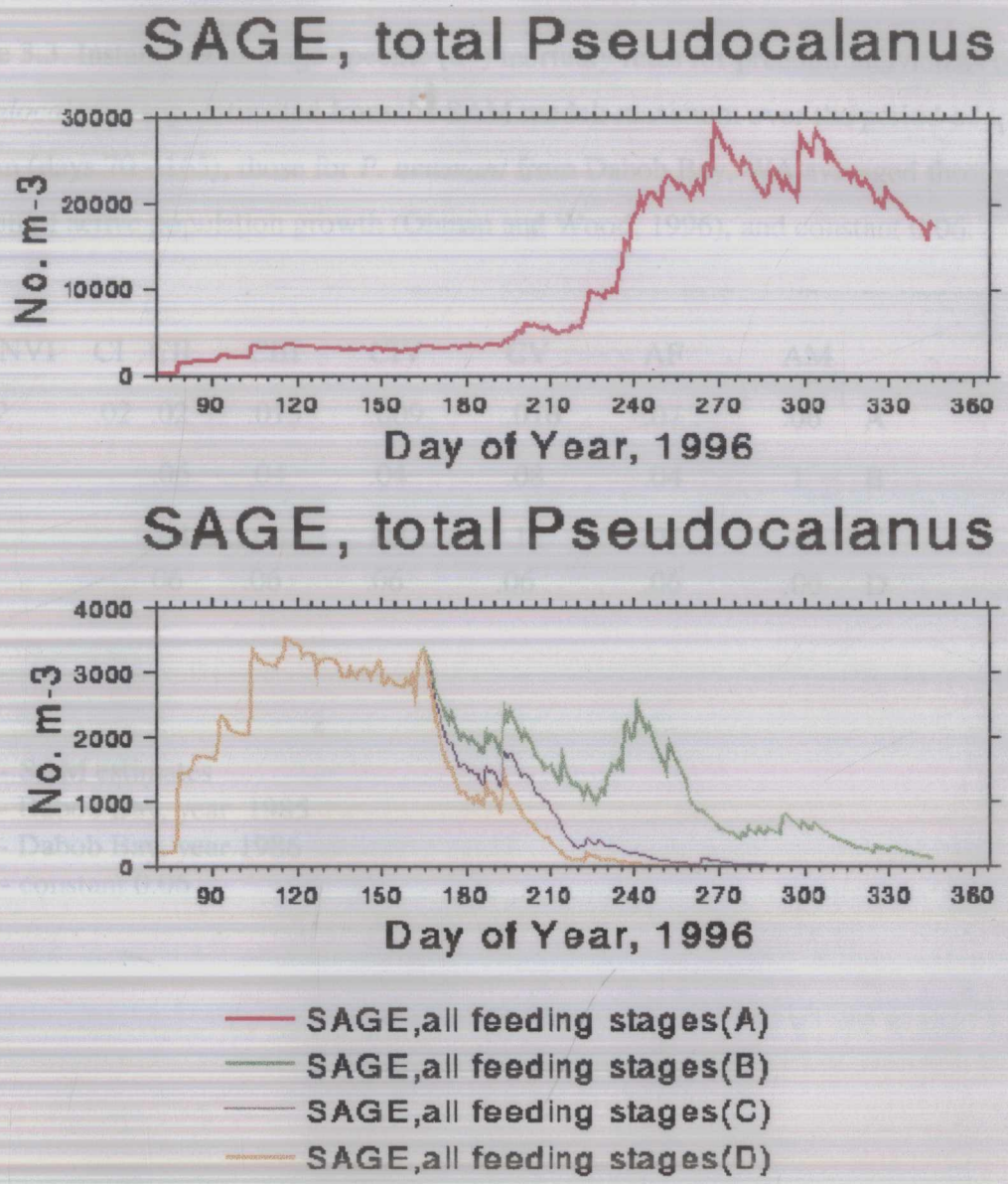

Figure 3.6. SAGE, abundance of *Pseudocalanus* spp. feeding stages. Mortality rates after day 165 were set: A) to the maximum of spring values; B) constant at 0.06; C), and D) after Ohman, Wood (1996) for the years 1985 and 1986 respectively.

Table 3.3. Instantaneous stage-specific (d^{-1}) mortality rates for preadult individuals of *Pseudocalanus* spp. estimated from the SAM model: maximum over the period of spring bloom (days 70 - 165), those for *P. newmani* from Dabob Bay, WA averaged through the season of active population growth (Ohman and Wood, 1996), and constant 0.06.

NI-NVI	CI	CII	CIII	CIV	CV	AF	AM	
.012	.02	.02	.013	.009	.016	.07	.06	A
.1		.06	.04	.04	.08	.04	.1	B
.12		.08	.06	.08	.12	.07	.17	C
06		06	.06	.06	.06	.06	.06	D

A - SAM estimates
B - Dabob Bay, year 1985
C - Dabob Bay, year 1986
D - constant 0.06

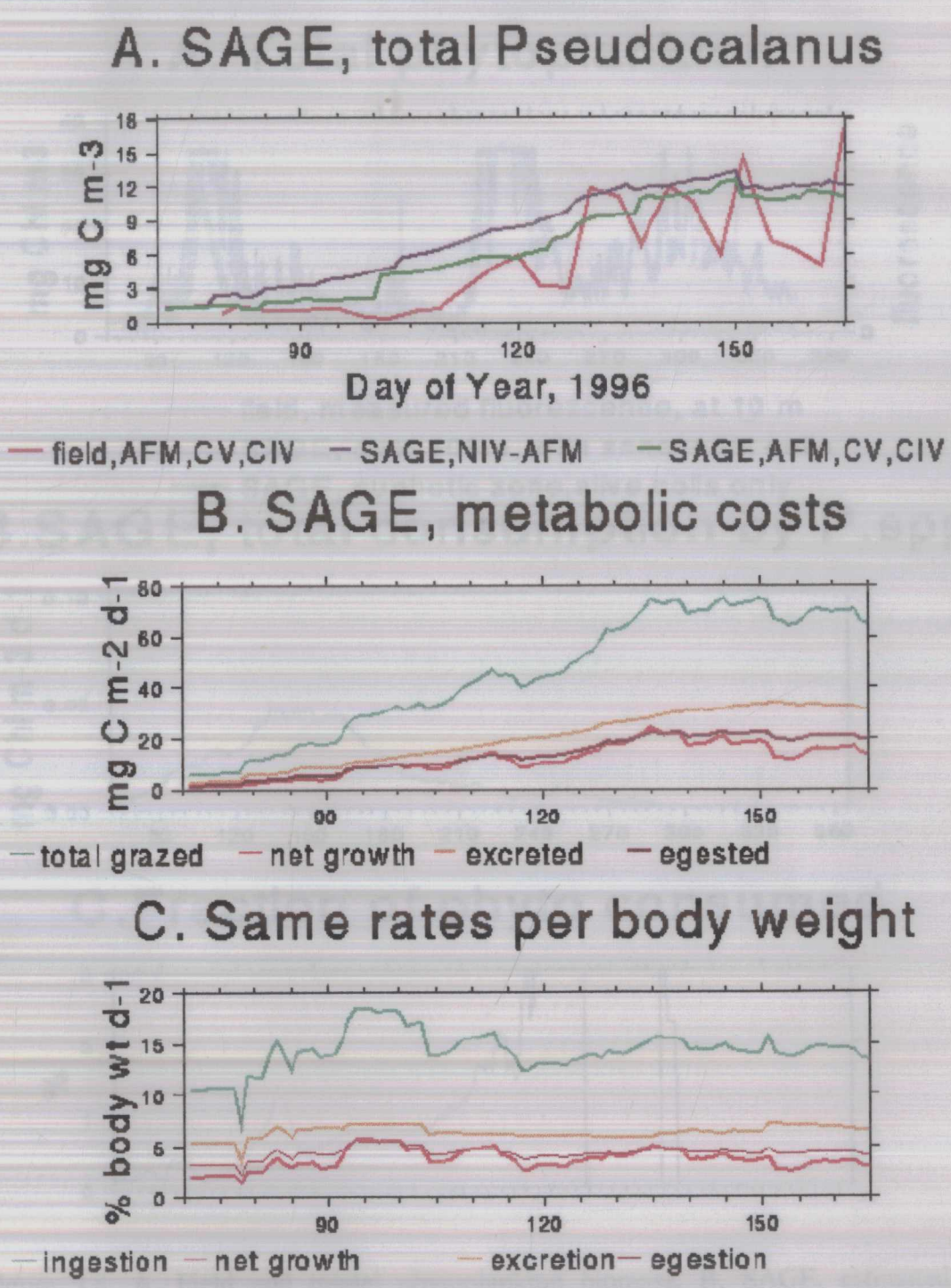

Figure 3.7. Total *Pseudocalanus* spp. abundance (A) and estimated metabolic costs, (B) instantaneous (d^{-1}), and (C) per body weight d^{-1}.

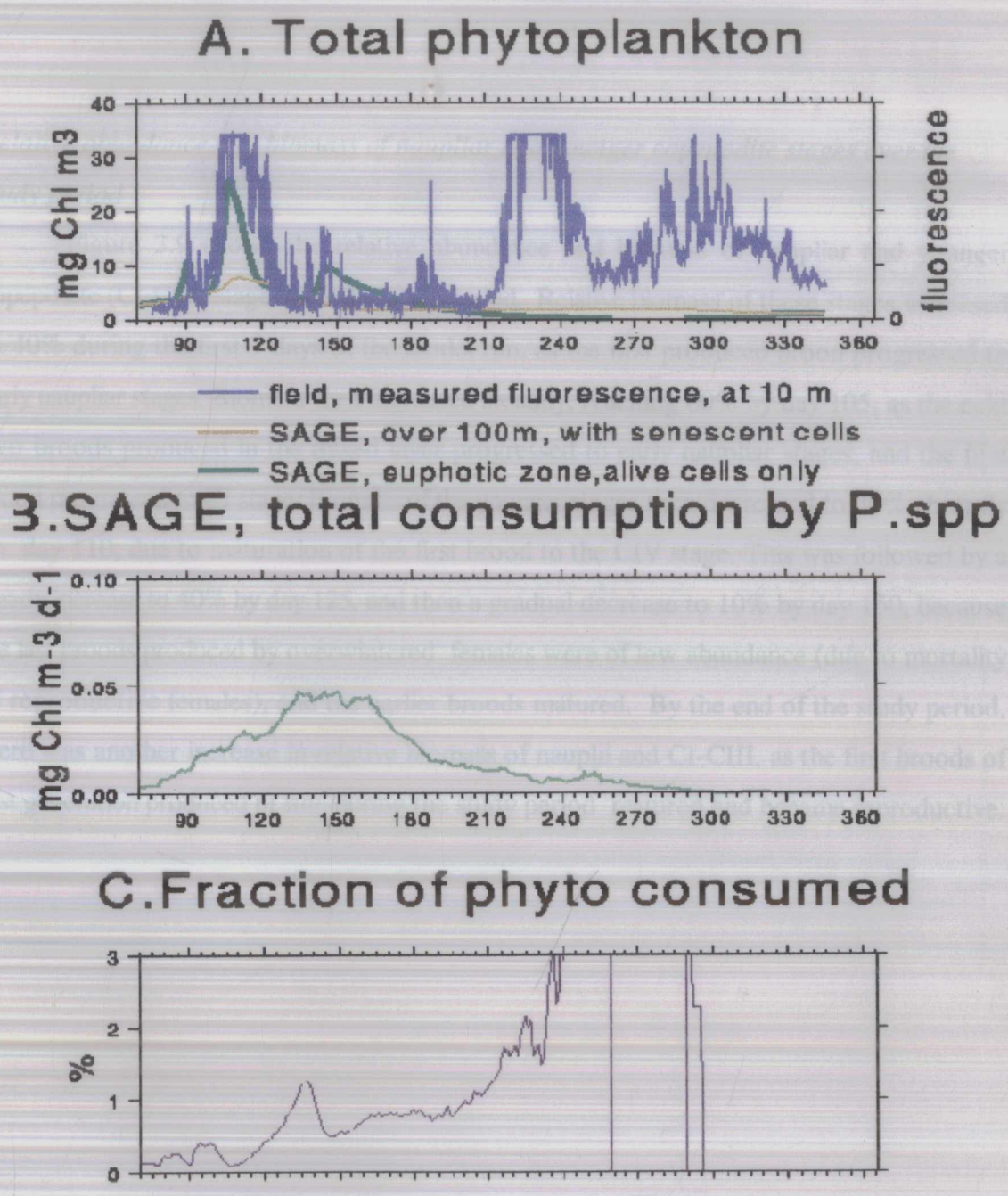

Figure 3.8. A. Field and model phytoplankton biomass. B. SAGE, estimated ingestion rate of *Pseudocalanus* spp. C. SAGE estimated fraction of phytoplankon consumed by *Pseudocalanus* spp.

Relative abundance and biomass of naupliar and younger copepodite stages over the study period

Figure 3.9 shows the relative abundance and biomass of naupliar and younger copepodite (CI-CIII) stages over the study period. Relative biomass of these stages increased to 40% during the first 7 days of the model run, as the first produced brood progressed to early naupliar stages. Biomass then increased steadily, reaching 60% by day 105, as the next two broods produced in the mixed layer progressed to early naupliar stages, and the first brood progressed to CI stage. Biomass of the younger stages then decreased to 30% abruptly on day 110, due to maturation of the first brood to the CIV stage. This was followed by a steady increase to 40% by day 125, and then a gradual decrease to 10% by day 150, because the last broods produced by overwintered females were of low abundance (due to mortality of reproductive females), and the earlier broods matured. By the end of the study period, there was another increase in relative biomass of nauplii and CI-CIII, as the first broods of first generation produced *in situ* during the study period matured and became reproductive.

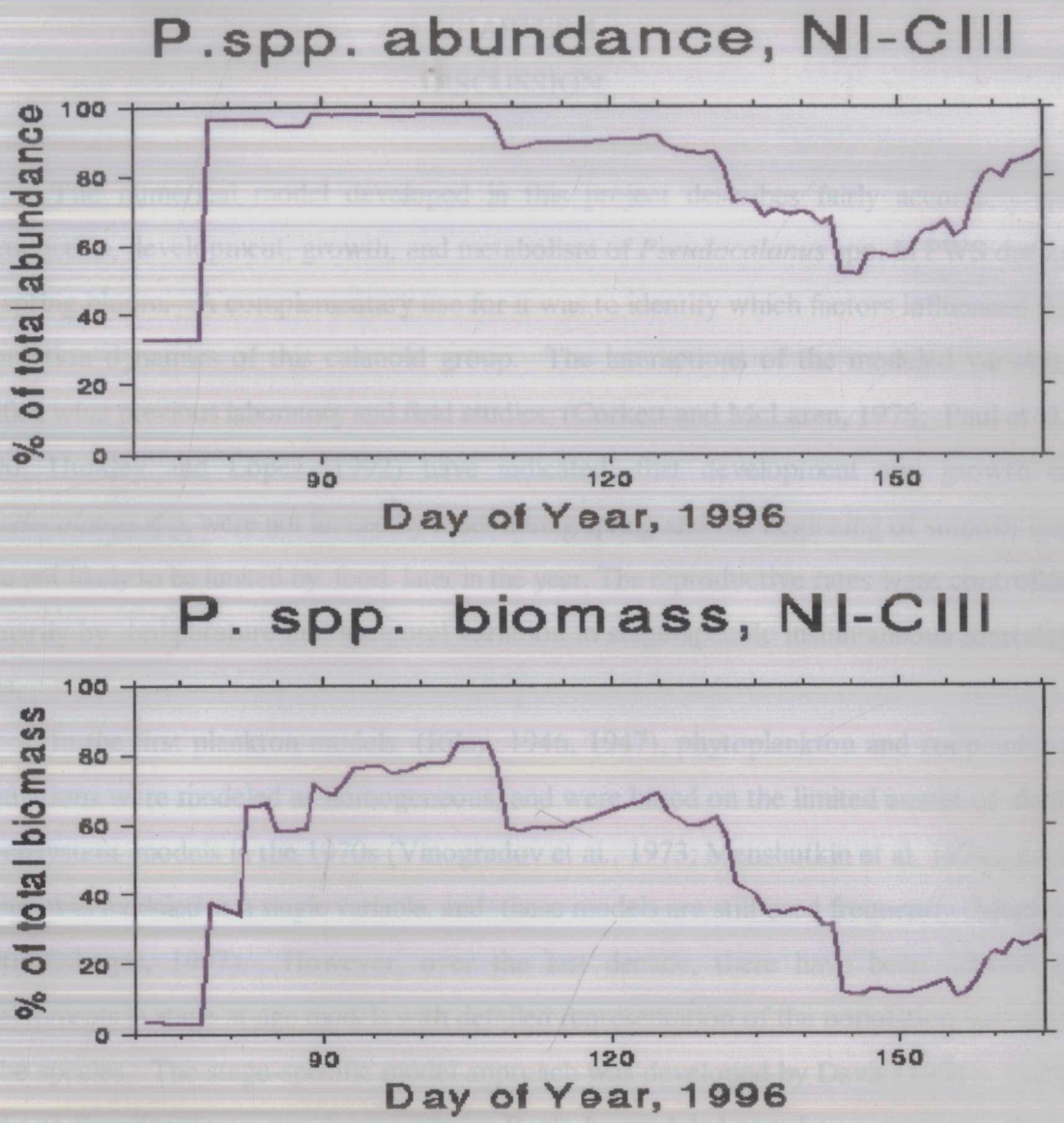

Figure 3.9. Relative abundance and biomass of naupliar (NI-NVI) and younger copepodite (CI-CIII) stages over the study period.

CHAPTER 4
DISCUSSION

The numerical model developed in this project describes fairly accurately the reproduction, development, growth, and metabolism of *Pseudocalanus* spp. in PWS during the spring bloom. A complementary use for it was to identify which factors influenced the population dynamics of this calanoid group. The interactions of the modeled variables verified what previous laboratory and field studies (Corkett and McLaren, 1978; Paul et al., 1990, Huntley and Lopez, 1992) have indicated: that development and growth of *Pseudocalanus* spp. were not limited by food during spring and the beginning of summer and were not likely to be limited by food later in the year. The reproductive rates were controlled primarily by temperature and temporal variation in stage-specific instantaneous mortality rates.

In the first plankton models (Riley, 1946, 1947), phytoplankton and zooplankton populations were modeled as homogeneous, and were based on the limited amout of data. In ecosystem models in the 1970s (Vinogradov et al., 1973; Menshutkin et al. 1974), each species was modeled as a single variable, and these models are still used frequently (Magley, 1990; Eslinger, 1997). However, over the last decade, there have been substantial developments in stage-at-age models with detailed representation of the population structure of the species. The stage-specific model approach was developed by Davis (1984). In his study of *Pseudocalanus* spp. from Georges Bank, he modeled population structure of this group with 13 state variables representing the abundance of all of the life stages. Development and daily egg production rates were food-unlimited and temperature-dependent and were estimated from Belehradec's equation. Stage-specific mortality, fecundity, and molting controlled the abundance and stage structure of the group. Stage-specific mortality rates were used to tune the model to fit field abundance data. Growth and metabolism were not considered. The model was coupled with an advection/diffusion model to examine the

spatial pattern of a copepod population.

Later model studies on calanoid copepods generally followed Davis' approach (Lewis et al., 1994; Lynch et al., 1998). Lewis et al. (1994) coupled a stage-specific generic copepod model with a wind-forced physical model of Georges Bank to confirm the wash-out hypothesis that wind-driven offshore advection resulted in reduction of zooplankton populations and, consequently, led to poor recruitment at higher trophic levels. Development was modeled as continuous and in a food-unlimited environment. At each time step abundance of each of the model stages was estimated as the number of individuals molted from the previous stage, less the number of individuals dying, less the number of individuals molting to the next stage. Metabolic processes and growth were not modeled. Egg production rates and molting rates were estimated from literature data on *Calanus* spp. Stage-specific mortality rates were estimated from Ohman (1986), but were constant and derived for a uniform 5°C water temperature. The *Calanus* represented the highest trophic level of the coupled biological model, which included phytoplankton and a dissolved nutrient pool. Grazing pressure of *Calanus* on phytoplankton was modeled by Ivlev's type grazing function (Lewis et al., 1994).

Lynch et al. (1998) developed a stage-based model of *Calanus finmarchicus* in the Gulf of Maine, and coupled the model with a nonlinear 3-D hydrodynamic model of the Gulf of Maine, to show that the first generation (G1) spawned in a food-rich area of Georges Bank and the copepods were advected into the food-poor Gulf of Maine surface layer. All life stages of *Calanus* were modeled and development was continuous and temperature-dependent, with stage durations estimated from Belehradec's function. Several food availability scenarios were tested. Mortality rates were stage-specific and constant through time. Metabolic processes were not modeled.

Batchelder and Miller (1989) developed an individual-based model to study life history and population dynamics of *Metridia pacifica* (Brodsky) from Ocean Station P. Their model was formulated so that growth of individuals of *M. pacifica* was food-limited, and

temperature effects were considered to be of minor importance and were not accounted for. Growth was estimated from the balance equation (assimilation less respiration), weight-specific grazing rates were estimated from a Michaelis-Menten type hyperbolic equation, reproductive parameters were chosen similar to those reported for other calanoid copepods, and mortality was estimated as a constant daily probability of predation. Vertical migration was not considered (Batchelder and Miller, 1989).

A coupled individual-based biological/physical model for the Georges Bank region was developed by Miller et al. (1998). An individual-based model of life history and life stage dynamics of *Calanus finmarchicus* was coupled with a tide- and wind-driven regional model of advection to show that all of the Gulf of Maine and the Scotian shelf contributed to the *Calanus* stock of Gorges Bank. The model predicted that the western part of the Gulf was restocked by the first generation produced at the western edge of the Bank as a result of the northward gyre circulation. At each time step, each individual of the *Calanus* model was the subject of spatial transition and stage-specific mortality; egg production rates and the duration of each stage were estimated from Belehradec's function, with parameters fitted to full-nutrition stage-duration *Calanus* spp. data. Metabolic processes were not modeled.

In the previous PWS NPZ model formulation (Eslinger, 1997), *Pseudocalanus* spp. was modeled as a single variable. In the present study, a stage-based approach was used similar to Davis (1994) and later works (Lewis et al., 1994; Lynch et al., 1998), with 15 development stages of *Pseudocalanus* spp. modeled, including eggs, all naupliar and copepodite stages, reproductive females, old nonreproductive females, and adult males.

Cohort analysis of the field data and the model output both indicated that reproduction and development were described well by Belehradec's temperature function with North Sea parameters. Development was synchronous, broods did not overlap, and the duration of each stage was proportional to the temperature-dependent embryonic duration using proportionality constants reported for Atlantic *Pseudocalanus* spp. The modeled PWS *Pseudocalanus* spp. produced broods in early spring, after overwintered females fed on the

spring phytoplankton bloom. The first generation matured and became reproductive by mid-June. The second generation matured by late summer and produced broods which progressed to the CV stage in October. Subarctic species of *Pseudocalanus* have a one year cycle (Corkett, McLaren, 1978), and model CVs must undergo diapause and overwinter, but the model was not tested for winter conditions.

The initial population structure and stage-specific mortality rates were calculated using the mixed layer temperature. However, generation times during the model runs were calculated using the model vertical temperature structure. Corkett and McLaren (1978) considered the effect of vertical temperature structure on ontogenetic migration of *Pseudocalanus* spp., and suggested the demographic hypothesis, which postulated that younger stages preferred warm surface waters to complete development to the CIII stage in a minimal time, whereas older animals and adult reproductive females migrated to deeper, cooler waters to gain a size advantage. However plausible the demographic hypothesis is, there is not enough information on vertically structured population abundance from PWS to test it. Cooney et al. (1999) found that the CV stage of *Pseudocalanus* spp. in PWS undergoes ontogenetic downward vertical migrations in May and June. Minoda (1971) found relatively uniform vertical distributions of *Pseudocalanus* spp. in the seas east of Kamchatka in the upper 50-200 m during May, June and July. No evidence was found for near surface concentration of nauplii in the Bering Sea (Paul et al., 1996); they were evenly distributed throughout the upper 30 m of the water column. In the SAGE model, all stages were distributed uniformly in the upper 40 m of the water column and vertical migration was not considered. In spring, all stages are probably actually distributed homogeneously in the mixed layer of PWS. However, as the water column becomes stratified later on in the year, if ontogenetic migrations do occur, they may have a substantial impact on the stage-specific abundances at different depths and influence the model estimates of total *Pseudocalanus* abundance integrated over depth.

The number of eggs per clutch, the number of clutches produced by a female during

its life span, and the initial abundance of reproductive females influenced the dynamics of modeled *Pseudocalanus* spp. substantially. The timing of the spring bloom and the initial abundance of overwintered females appear to be more important factors than temporal variation in egg production rates, and would probably result in differences in total *Pseudocalanus* biomass between years. Paul et al. (1990) found that interannual differences in *Pseudocalanus* female abundance in Auke Bay, Alaska, at the time that larval pollock began feeding on nauplii, were more important in determining naupliar abundance than changes in egg production rates. In the SAGE model egg production rates did not vary with time. Good agreement between the model and field data was achieved when the number of eggs per clutch was set to 5, which was close to the average of 2.6 eggs female^{-1} day^{-1} estimated for 1987 and 1988 in Auke Bay, southeastern Alaska (Paul et al., 1990). In that study, it was found that egg production rates were time-dependent and that weekly estimates of egg production rates were 1.4 -15.4 eggs female^{-1} day^{-1}. Rates were lower in April than in in May (6.9 vs 9.0 in 1987 and 3.2 vs 11.4 in 1988). In the present model the abundance of all stages was somewhat overestimated early in the study period compared with the field data, and somewhat underestimated later in the study period, which may have resulted from keeping egg production rates constant through time.

Stage-specific mortality rates were derived from the SAM model for the period of time when field data were available. They provided reasonable SAGE estimates of abundance of *Pseudocalanus* spp. on stage-specific basis (Figure 3.6).

Early in the study were several periods of increased mortality in early development sages, most likely due to natural mortality due to unfavorable environmental conditions. In April (days 100-120) AFK stage-specific mortality rates were relatively low, apparantly due to decreased natural mortality and low abundance of predators in spring (SEA 1996; Dagg et al., 1983). After day 120 (beginning of May), daily mortality rates for naupliar stages often increased, at times reaching 0.09d^{-1}. Increased mortality was also observed for younger copepodite stages CI-CIII; around day 145 and later, naupliar and CI-CIII rates reached 0.06

- $0.09d^{-1}$. These increased *Pseudocalanus* mortality rates coincided with a pink salmon fry release from the AFK hatchery (May 24). Approximately 12.46 million fry were released at an average weight of 0.7 mg each (Ferren and Milton, 1997), which could have a substantial impact on mortality rates of *Pseudocalanus* spp. However, in a recent study on the feeding ecology and growth of juvenile pink salmon, Parker (1997) found that pink salmon fry had a diet preference for the larger copepods of the *Neocalanus/Calanus* group and euphausiids.

Parker (1997) calculated Ivlev's selectivity coefficients for pink salmon fry in order to relate the stomach content to zooplankton abundance, based on data from 20 m vertical tows at AFK in 1994. The Ivlev's selectivity coefficients showed an overall negative value for calanoids, the dominant zooplankton, indicating that they were not taken by pink salmon fry in proportion to their availability. The *Neocalanus/Calanus* group exhibited an overall positive coefficient, as did the euphausiids, and harpacticoids (Parker, 1997). Cooney and Coyle (1997) have shown that *Neocalanus* spp. (stages CIV-CV) were the top three taxa in western PWS during May 1996 by abundance, followed by *Pseudocalanus* spp. (stage CV, and adult females), *Neocalanus* spp. (stage CIII, and CIV), *Calanus marshallae* (stages CII and CIV), and euphausiids.

Increased naupliar and early copepodite mortality in May also may be the result of an increase in abundance of suspension feeding zooplankters in Prince William Sound. Stage-specific variability in instantaneous mortality rates for the last three weeks showed a bimodal pattern similar to that reported for *Pseudocalanus newmani* from Dabob Bay (Ohman and Wood, 1996). Mortality rates were higher for naupliar and copepodite stages CI-CIII, low for copepodite CIV, and increased again for stage CV. Some of these trends in mortality may be artifacts of the model rather than real trends. However, Ohman (1986; 1990) and Ohman and Wood (1996) hypothesized that low mortality rates for CIVs may result from better avoidance by these stages of the suspension-feeders *Euphausia pacifica*, *Metridia pacifica*, *Calanus pacificus*, and possibly *Oithona similis,* which prey heavily on *Pseudocalanus* nauplii and early copepodite stages. Suspension feeding zooplankters of the

euphausiid group were among the ten most abundant taxa in PWS in May 1996 (Cooney and Coyle, 1997). Increased mortality of CVs and adults may result from high vulnurability of these stages to predation by carnivorous zooplankton (Ohman and Wood, 1996). A carnivorous copepod, *Euchaeta elongata*, and a chaetognath, *Sagitta elegans* are potential predators on the CV stage in PWS; a carnivorous hydromedusan, *Aglantha digitale,* ranked among the top 10 taxa for PWS in May 1996 (Cooney and Coyle, 1997).

Mortalities for the early development stages of *Pseudocalanus* spp. may be high in June due to predation by Pacific herring larvae. The period of growth and metamorphosis of Pacific herring larvae coincided with the period of maximum copepod nauplii production in Auke Bay, South-central Alaska (McGurk et al., 1993). Hay et al. (1988) found that predation by herring larvae markedly affected nauplii abundance in enclosed populations of Atlantic *Pseudocalanus elongatus.* Bollens (1988) came to the same conclusion working with a population dynamics model of *Pseudocalanus* spp. and herring larvae data from Dabob Bay. However, in several Bering Sea studies on pollock (Dagg et al., 1984) and herring (McGurk et al., 1993) larvae, no evidence was found for any impact on nauplii abundance. In Auke Bay, a steady increase in nauplii abundance was found in April-June during 1986 and 1988, but in 1987 and 1989 they declined in June (Paul et al., 1991), which could be due to fish predation.

SAM daily mortality rates for adult reproductive females were low (0.02 d^{-1}) in spring, increasing to 0.07d^{-1} once at the end of April and then peaking again in May and June (Figure 3.5). One possible explanation is that planktivorous fish may select reproductive females, which are large and easy to see with egg sacs. One would expect that fish would prefer to prey on adult females with egg sacs rather than on small nauplii, because the females would provide more energy. For example, capelin in Auke Bay fed preferentially on adult female *Pseudocalanus* spp. in late May and June (Coyle and Paul, 1992). I expect *Pseudocalanus* spp. CIV-CV and adult stage-specific mortality rates to be significantly higher later in summer when all the planktivorous young-of-the-year fish, such as herring,

pollock, and capelin will have metamorphosed and will be heavily preying on *Pseudocalanus* spp. It was shown (Hillgruber et al., 1995) that young pollock grow 0.4 mm per day, and they must have a tremendous consumption rate to achieve this level of growth. In PWS newly metamorphosed pollock eat 9-10% of their body weight per day when feeding on copepods (Paul et al., 1998).

When field data were not available, I used reported stage-specific mortality rates for *P. newmani* from Dabob Bay for two different years (Ohman, Wood, 1996) to test the sensitivity of the model to these parameters, as well as to test the hypothesis of food unlimited growth of *Pseudocalanus* spp. later in the year. The model was sensitive to these parameters; Dabob Bay rates for the year 1986 were about 2 - 3% higher than those for the year 1985 which resulted in higher abundance of modeled *Pseudocalanus* spp. These results suggest that stage-specific mortality may be the key factor controlling *Pseudocalanus* spp. abundance and a source of interannual variability in population abundance and biomass of this genus. These results also suggest that stage-specific mortality rates should be substantially higher later in summer and fall due to predation pressure. However, the thermal regime and predator fields in Dabob Bay would differ considerably from those of PWS, so mortality rates may be radically different for the two sites. Prince William Sound rates may be lower, because applying Dabob Bay rates to modeled PWS *Pseudocalanus* resulted in the extinction of the model population by Julian day 270 (the end of September). Little can be said about the predation pattern later in the year, because field data were not available.

In formulating the model of *Pseudocalanus* spp. the central assumptions were that the growth of this group, like that of other marine copepods, may be described by a weight-specific exponential function of temperature, and that the population grows at its maximum rate in a food satiated environment (Huntley and Lopez, 1992). The estimated net growth rate for total *Pseudocalanus* was about 5% of body weight per day during the study period (Figure 3.7C), lower than the 10-17% reported for older stages (Corkett and McLaren, 1978), because the present growth rates were net rates, and did not account for the excretion

term. Metabolic costs estimated as percent of body weight per day from the allometric equation for the Bering Sea zooplankton community (Dagg et al., 1982) were equal to 5% (Corkett and McLaren, 1978). Given an egestion rate of 30% of assimilated food, an ingestion rate was estimated from the balance equation. The ingestion rate was equal to about 20% per body weight d^{-1}, near range of 2.6 -12.1% (Zagorodnaya, 1974, cited by Corkett and McLaren, 1978), and within the range of 2.2-55.5% (Poulet, 1975, 1977, cited by Corkett and McLaren, 1978) for *Pseudocalanus* in natural conditions. The ingestion rate of model *Pseudocalanus* increased by the end of the study period to about 80 mgC m^{-2} d^{-1}, as broods progressed to older stages. In field measurements, the maximum spring bloom ingestion rates were 25.6-69.5 and 597.8-1825.3 mgC m^{-2} d^{-1} for large copepods, and for all zooplankton for the Bering Sea middle-shelf domain, respectively, and total zooplankton consumption was 70.3-94.0 mgC m^{-2} d^{1} for the coastal domain (Dagg et al., 1982). Estimates for *Pseudocalanus* alone were not available. The ingestion/primary productivity ratio (I/P) for the coastal domain of the Bering Sea was 4.9-6.5% for all zooplankton, and the model *Pseudocalanus* (I/P) ratio was about 1.5% by day 130, as maturing broods grazed effectively. The ratio then decreased to less than 1% from day 180 to 210, in the postbloom deficient conditions. Abundance of zooplankters was also low, most likely due to predation on younger stages at some earlier time. The model I/P ratio increased by day 240 to 3% and higher, as model phytoplankton concentrations were very low.

Modeling zoplankton metabolic processes resulted in more accurate estimates of the nutrient and detritus pools of the coupled biological model by including sources of ammonia and fecal material. Stage-specific growth and stage-(weight) specific metabolism also allowed estimation of stage-specific grazing pressure and the total amount of phytoplankton consumed. Consumption was a small fraction of modeled total phytoplankton over the study period. Fluorescence data (a widely accepted, yet approximate, indicator of total phytoplankton biomass) were used in comparisons with model phytoplankton. Spring phytoplankton time series (surface mg Chl m^{-3}) were available from AFK site (McRoy et al.,

1997), and were in a good agreement with fluorescence C-LAB data (10 m depth) in timing, but were of somewhat lower magnitude. The AFK time series and C-LAB data agreed in the timing and magnitude of the postbloom period. At the AFK site, the diatom *Chaetoceros* spp. was most abundant at all depths during the postbloom period. The relative abundance of the small diatom *Skeletonema costatum* increased during a short recovery of the bloom in June (McRoy et al., 1997). Flagellates comprised 65% of the carbon biomass in May, and *Rhizosolenia fragilissima* was the dominant species by carbon biomass during the June recovery (Ward, 1997). C-LAB data indicated a substantial increase in phytoplankton biomass in August (Julian days 213-240), and in October-November (Julian days 275-330), but species composition and the nature of these blooms are unknown. The increased phytoplankton biomass could be attributed either to mixing events and nutrient enrichment leading to a bloom, or to a measurement artifact associated with the genus *Phaeocystis*.

To tune the model to the field data, the method of Ohman and Wood (1994) was used to estimate instantaneous, time-dependent, stage-specific mortality rates from the field data. SAM derived mortality rates for nauplii and younger copepodite stages may not have been estimated accurately, since the 333 μm mesh net undersampled CI-CIII stages, and information on their abundance was not used in the bicubic interpolation. Because egg abundance was not measured, it was estimated from adult female numbers and the time between successive clutches, which is another potential source of error. The effect of advection on the stage-specific mortality rates estimated from the field data, even taking into account that the advection signal is minimal during spring and summer (Niebauer, 1994), could have been significant. The late spring and early summer stage-specific mortality rates were probably underestimated due to advection, as all the observations over this period of time suggest that predator abundance in PWS was high. Field-derived stage-specific mortality rates, however, were the best estimates available. Future efforts linking the present model with a fully three-dimensional model would allow the effects of advection to be determined.

Modeling stage-specific growth rates using the exponential function suggested by

Huntley and Lopez (1992), I took mean stage-specific weight estimates from spring AFK data for *Pseudocalanus* spp. Actually, two populations were present in the system: larger animals and smaller animals (Coyle, Cooney, personal communication). As their relative abundance was not known, I took weights of the larger population as model weights. It was also known from the observations (Coyle, Cooney, personal communication) that *Pseudocalanus* spp. were smaller during summer time, but as no weight estimates were available later in the year, I kept the spring weight values as model values when running the model on an annual basis.

In future efforts, coupling the SAM and SAGE models could provide more information about predation *in situ* if all copepodite stages are sampled accurately and possible effects of advection are determined. The frequency of sampling for the AFK population abundance data was high: every 2 - 5 days. Using the AFK field data allowed the calculation of the PWS spring stage-specific instantaneous mortality rates, which were found to be variable between the stages. It would be interesting to perform Monte Carlo tests of the method's efficacy (Wood, 1994) and to estimate the optimal frequency of sampling. Given the good agreement between field and model temperatures over the study period, using the SAGE temperatures of the mixed layer allowed the age structure of the sampled stage-structured population to be estimated. A good agreement between SAGE and field temperatures was achieved over the spring study period, but later in the year the model temperature of the deeper water was underestimated, as the 1D model did not account for warming of the deeper layers, perhaps as a result of advection. Coupling the SAGE and the SAM models with a 3D circulation model could make the temperature estimates more accurate. Coupling the 1D biophysical model with a circulation model could provide valuable information about the spatial and temporal distribution of *Pseudocalanus* populations in Prince William Sound.

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